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Author contributions statement

S.J.D and A.W conceived the experiments. S.J.D conducted the experiments and analyzed the results. S.J.D and A.W wrote the manuscript. S.J.S, S.P.L and L.A.W. provided essential logistical support. All authors reviewed the manuscript.

Abstract

Cumulative culture is rare, if not altogether absent in non-human species. At the foundation of cumulative learning is the ability to modify, relinquish or build upon prior behaviors flexibly to make them more productive or efficient. Within the primate literature, a failure to optimize solutions in this way is often proposed to derive from low-fidelity copying of witnessed behaviors, sub-optimal social learning heuristics, or a lack of relevant socio-cognitive adaptations. However, humans can also be markedly inflexible in their behaviors, perseverating with, or becoming fixated on outdated or inappropriate responses. Humans show differential patterns of flexibility as a function of cognitive load, exhibiting difficulties with inhibiting sub-optimal behaviors when there are high demands on working memory. We present a series of studies on captive chimpanzees which indicate that behavioral conservatism in apes may be underlain by similar constraints: chimpanzees showed relatively little conservatism when behavioral optimization involved the inhibition of a well-established but simple solution, or the addition of a simple modification to a well-established but complex solution. In contrast, when behavioral optimization involved the inhibition of a well-established but complex solution, chimpanzees showed evidence of conservatism. We propose that conservatism is linked to behavioral complexity, potentially mediated by cognitive resource availability, and may be an important factor in the evolution of cumulative culture.

Keywords: Behavioral flexibility, cumulative culture, chimpanzee, comparative psychology, learning, decision-making

Human culture is extraordinarily flexible in nature, exemplified by extensive diversification in technology and social practices. Behavioral flexibility forms not only the bedrock of this diversity but is a vital prerequisite for cumulative culture, affording the ability to build on established behaviors by modifying old solutions, and flexibly switching to more productive or efficient ones. Yet, our closest living relatives, chimpanzees, are reported to show difficulty in changing their solutions despite the availability of superior alternatives. This has been suggested to be an important explanation in that despite the existence of multiple-tradition cultures that include an extensive diversity of forms of tool use, chimpanzees show minimal evidence at best of the cumulative evolution that that has shaped so much of human culture (Tennie, Call & Tomasello, 2009; Whiten, Hinde, Laland & Stranger, 2011; Whiten, McGuigan, Marshall-Pescini & Hopper, 2009). Understanding the nature of behavioral conservatism, whereby prior knowledge appears to block or delay adoption of an alternative behavior (Lehner, Burkart, & Schaik, 2011; Marshall-Pescini & Whiten, 2008), may help explain the relatively static and limited scope of chimpanzee culture. In contrast, human cumulative culture is typified by modifications to existing, and often complex sequences of behavior that underwrite our technologies, languages and social customs.

1.1 Cognitive accounts of behavioral inflexibility in humans

Given the adaptive advantage of behavioral flexibility in solution optimization (convergence on the most productive or efficient behaviors), why would any species exhibit highly conservative tendencies? Strikingly though, inflexibility in action or thought is well documented in human children (e.g. Defeyter & German, 2003; Kirkham et al., 2003; Zelazo et al., 2003), as well as in human adults (e.g. Bilalić et al., 2008a, b; Chrysikou et al., 2013; Diamond, 2005; German & Barrett, 2005; Gopnik et al., 2015; Luchins, 1942; Pope et al., 2015; Wiley, 1998). Within this human literature, the phenomenon is more often referred to in relation to concepts of perseveration, functional fixedness or mental set (aka *Einstellung*).

We suggest that perseveration analyzed in the human literature, and behavioral conservatism described in the non-human primate literature, exhibit parallels: both involve the continued use of outdated responses despite knowledge of a more appropriate alternative. In contrast, functional fixedness, or mental set, tends to be more closely linked with (lack of) innovation, creative thinking, or insight, specifically getting 'stuck' on the common usage of a tool or behavior pattern, blocking solutions which would otherwise be easily generated (Defeyter & German, 2003), a blockage overcome once knowledge of an alternative becomes available.

Perseveration

Perseveration in children is linked to the development of executive functions: "a set of general-purpose control mechanisms … that regulate the dynamics of human cognition and action" (Miyake & Friedman, 2012, pg 2). While there is some disagreement concerning the nature of executive functions, commonly identified components include inhibition (overriding "a strong internal disposition"), working memory ("holding information in mind and mentally working with it") and switching/shifting ("changing perspectives or approaches to a problem") (Diamond 2013, pg137). Allocation of resources to executive functions comes increasingly under control with age (Best & Miller, 2010; Braet et al., 2009; Thompson-schill, Ramscar, & Chrysikou, 2009), with maturation linked to both increases in working memory capacity and inhibitory control (Diamond & Doar, 1989).

From the executive function perspective, we expect the likelihood of perseveration to be affected by two mechanisms: (i) response prepotency, and (ii) working memory load (Grandjean & Collette, 2011; Roberts, Hager, & Heron, 1994; Roberts & Pennington, 1996). (i) Extensive practice with behavior may cause it to become a predominant or prepotent response (Miller, 2000), making it difficult to subsequently relinquish through inhibitory processes. (ii) Increased taxation or load on working memory, associated with complex behavior, affects the ability to adopt solutions (Beilock & Decaro, 2007; See also Gathercole et al., 2008). Crucially, not only might these two factors affect the likelihood of perseveration, but may share cognitive resources i.e. draw from the same finite pool of the brain's computational power (Barber, Caffo, Pekar & Mostofsky, 2013; Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Chambers, Garavan, & Bellgrove, 2009; Hester, Murphy, & Garavan, 2004; McNab et al., 2008; Mostofsky et al., 2003). For example, increased load on working memory is associated with greater difficulties in successfully inhibiting behaviors and adopting alternatives (Berger, 2004, 2010; Chmielewski, Mückschel, Stock, & Beste, 2015; Conway, Cowan, & Bunting, 2001; Davidson, Amso, Anderson, & Diamond, 2006; Grandjean & Collette, 2011; Hester & Garavan, 2005; Roberts et al., 1994; Stedron, Sahni, & Munakata, 2005; see also Kane & Engle, 2003; Marton, Kelmenson, & Pinkhasova, 2008; Redick, Calvo, Gay, & Engle, 2011). These studies indicate that the more prepotent and complex an existing response, the greater the difficulty in relinquishing this response and adopting another (Houghton and Tipper, 1994; Munakata, 2001). Importantly, this research strongly suggests that behavioral conservatism is a function of cognitive resource availability: perseveration is underlain by limited cognitive resources in key executive functions, with high demands on working memory likely detracting from the resources needed for inhibition.

A cognitive account of behavioral inflexibility in chimpanzees

Behavioral conservatism in primates is typically ascribed to some limitation in their social learning capabilities, such as low-fidelity copying (Lewis & Laland, 2012), or lack of relevant socio-cognitive adaptations (Tomasello, Carpenter, & Hobson, 2005); however, the present study of the context of behavioral flexibility in chimpanzees leads us to contend that chimpanzees display behavioral conservatism under the same conditions that cause perseveration in humans. We re-examine behavioral conservatism through a cognitive lens (see also Gruber, 2016; Gruber, Zuberbuhler, Clement & van Schaik, 2015) by drawing from the human literature to advance a relatively unexplored cognitive account of why we observe behavioral inflexibility in our close primate cousins. We propose that this new and complementary way of thinking about behavioral conservatism helps explain the mixed findings within the primate literature, and additionally, offers important insights into the relatively static nature of chimpanzee culture.

Behavioral conservatism in chimpanzees

There is no unitary concept of what makes one behavior complex and another simple, but we propose two metrics for which we might reasonably assume complexity. The first concerns the learning of new behavioral processes; individuals familiar with simple mechanics, such as levers, or sliding doors, do not need to relearn *how* to pull or slide when confronted with novel problems requiring these responses. They must only learn the particular affordances of the new problem and then apply known behaviors (Byrne & Russon, 1998). In contrast, solutions which require novel action elements must be learnt through some form of process learning. Therefore, in these studies, we class simple behaviors as those which are already well within the capabilities of the participants, and easily discovered by novices. Second, we might assume behaviors which require holding in memory several relations between objects, such as solutions involving multiple, non-arbitrary steps, are more complex than solutions which require fewer steps, with the former placing higher demands on cognitive resources (Halford, Wilson, & Phillips, 1998). As such, we consider these solutions, which are not easily adopted by novices, and which require relatively long periods of learning before mastery, as complex.

When solutions involve simple behaviors, chimpanzees have been found to modify well-established behaviors to improve productivity and efficiency. For example, Hopper et al. (2015), van Leeuwen, Cronin and Schutte (2013) and Vale et al (2017) found that chimpanzees in token deposit and token exchange tasks flexibly switched between solutions to maximize payoff. However, the initial solution (Solution A) in these studies, and the new, more productive alternative solution (Solution B) were not only relatively simple behaviors but conceptually very similar to one another - B involved the same behaviors as A, with the exception of changing the type of token exchanged or the location the token was deposited. These behaviors likely place low cognitive demands on participants (see also Manrique, Volter & Call, 2013). Relatedly, when Solution A is not prepotent, there is also evidence that chimpanzees will quickly relinquish solution A for B. For example, Horner and Whiten (2005) first demonstrated a complex Solution A to young chimpanzees, who upon discovering the redundancy of some elements of A, modified it to display a simpler, more efficient variant (B). However, chimpanzees practiced A only three times before using B, so A was not a well-established solution (see also Yamamoto, Humle & Tanaka, 2013). In contrast, chimpanzees show difficulties in adopting, relinquishing or building upon behaviors when higher levels of solution complexity are involved and the initial solution is well-established. For example, Davis, Vale, Schapiro, Lambeth and Whiten (2016), Hrubesch, Preuschoft and van Schaik (2009), and Marshall-Pescini and Whiten (2008) found that under these conditions, chimpanzees failed to change, build upon or fully relinquish Solution A in order to adopt a more optimal Solution B, despite B being within their behavioral repertoires. Thus, when Solution A is both complex and prepotent, chimpanzees appear to display high levels of perseveration with Solution A.

Given these findings, we propose that chimpanzee behavioral flexibility may be context dependent, with factors such as response prepotency and complexity of behavior affecting the likelihood of behavioral change, and thence behavior optimization. While executive function processes and problem solving capabilities have been examined in captive chimpanzees (Amici, Aureli & Call, 2008; Beran, Washburn, & Rumbaugh, 2007; Evans, Perdue, & Beran, 2014; Manrique & Call, 2015; Seed, Call, Emery, & Clayton, 2009; see also Seed, Seddon, Greene, & Call, 2012; Vlamings, Hare, & Call, 2009), to our knowledge, we are the first to propose this executive function framework of behavioral conservatism in chimpanzees, and to provide direct evidence below in support of this new, cognitive based account of context dependent flexibility.

The present study

To explore the hypothesis that chimpanzee behavioral conservatism may be underlain by cognitive constraints similar to those demonstrated in human research, we presented captive chimpanzees with solution optimization puzzles. We trained captive chimpanzees to adopt sub-optimal techniques. Solution optimization required inhibiting these techniques to adopt a more productive alternative. One puzzlebox (the 'Biways box') involved only simple behaviors, whereas a second ('Pitfall box') involved a mixture of complex and simple solutions. We assumed that complex behaviors would be associated with a higher cognitive load, and thus expected chimpanzees to show greater difficulties with inhibition in that case.

With a focus on the effects of solution complexity on behavioral flexibility, we aimed to answer the following questions:

I. Study 1.1. Biways box: Will chimpanzees inhibit an established but *simple* solution and switch to a *simple* alternative to increase reward pay-off?
II. Study 1.2. Biways box: Does having an established but *simple* solution hinder adoption of the *simple*, more productive alternative?
III. Study 2.1. Pitfall box: Does having an established but *complex* solution (Solution A) hinder adoption of a more *complex*, more productive solution (Solution B) when inhibition of A is *not* required
IV. Study 2.2. Pitfall box: Does having an established but *complex* solution (Solution A) hinder adoption of a *simple*, more productive alternative (Solution C) when inhibition of A is required?

Study 1.1 Biways box: Will chimpanzees inhibit an established but *simple* solution and switch to a *simple* alternative to increase reward pay-off?

Rewards in the Biways box could be attained via the operation of one of two handles distinguished by both location and coloring, as well as the action required to operate them (Figure 1). Operating the top handle (slide handle) delivered one peanut (Supplementary video 1), whereas the bottom handle (pull handle) delivered a higher value payoff, the peanut plus 2-3 grapes, the latter being a highly valued food reward for chimpanzees (Supplementary video 2). Both methods were single-stepped and well within the participant's repertoires. Accordingly, we class these as relatively 'simple solutions': they do not require learning new behavioral processes or holding multiple relations in mind.

Insert Figure 1 about here

Chimpanzees across five groups first learned the slide solution. In three of these groups, a conspecific group member (the model) then demonstrated the more productive pull technique (increased payoff with social information – IPSI – groups). To determine if behavioral change within IPSI groups was motivated by payoff, in the remaining two groups, a model also introduced the pull technique, but this pull solution produced the same reward as the slide solution (i.e. there was no payoff incentive to change to this new technique – same payoff with social information – SI - groups).

Given the importance of social learning for the propagation, maintenance, and accumulation of culture (Boyd & Richerson, 1996; Legare & Nielsen, 2015), we examined the effects of social information on behavioral optimization through the inclusion of an asocial control condition. Here, individuals experienced the same puzzlebox configuration as the IPSI group, but no social information was available regarding the more productive pull technique (increased payoff but no social information - IP - individuals). Group conditions are summarized in Table 1.

Insert Table 1 about here

Methods

Participants

Twenty-eight chimpanzees participated (9 males; average age: 31.7 years; range: 13.09 – 50.39) and were group housed at the National Center for Chimpanzee Care at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop, Texas, U.S.A. See Supplementary Materials Table S1 for further participant details.

Apparatus

The Biways box, originally designed for a comparative social learning study (Wood, Kendal, & Flynn, 2013), was re-purposed by SJD for the current study. No participant had previous experience with this box. Additionally, the Biways box was significantly modified from its original form, both in appearance and function. It was transparent with the two handles protruding from the front. When the slide handle was slid to the right, it knocked a peanut off a shelf inside the apparatus, and down a chute, where it could be retrieved by the participant. Alternatively, the pull handle could be used to displace the entire shelf so that all of the greater reward (nut + grapes) fell down the chute. The reward on the shelf was always visible to the participant.

Training phase

Increased payoff with social information (IPSI) groups. 25 individuals across three groups were given five hours of opportunity to train, where an already-trained, mid-high ranking, female conspecific demonstrated the slide solution to produce one peanut within her group. Of these 25 individuals, eight met criterion for inclusion (range of 2-3 individuals per group). The pull handle was locked so that it was immovable (thus making the grapes unobtainable). Participants were considered to have established the slide technique when they slid the handle fifty times over three separate training sessions, with no more than two touches to the pull handle (with the count reset at every third touch). Such a strict criterion ensured that not only was the slide solution a well-established response, but that any pull responses in subsequent testing were unlikely to be spurious, or 'accidental'. If an individual showed interest in participating but was unable to complete training to criterion within the five hours, they were offered the opportunity to voluntarily enter their indoor enclosures and separate for further training. Due to the high inclusion criterion, further training was required for all but one individual.

Same payoff with social information (SI) group. Training with two groups (total of 13 individuals with N=6 meeting criterion for inclusion) followed that outlined above, with the exception that the Biways box was baited with only one peanut.

Increased payoff but no social information (IP) group. Five individuals were offered the opportunity to separate for training with a human demonstrator, with the criterion for inclusion as outlined above. The box was baited with one peanut and three grapes, but only the peanut could be retrieved via sliding the handle. The pull handle was locked shut. Human demonstrations of the slide technique were given.

Testing phase

Increased payoff with social information (IPSI) group. The pull handle was unlocked. Following model retraining, over ten hours of testing, the model now demonstrated the pull solution. All participants observed the model before participation, and could participate throughout this testing phase (Table S5). Participants could thus solve the Biways box by sliding the slide handle (for one peanut) or could switch to pulling the more productive pull handle.

When the participant removed the reward from the chute, the apparatus was immediately pulled away, reset and rebaited.

Same payoff with social information (SI) groups. Testing followed the procedure above, with the exception that the pull handle resulted in the same reward as the slide handle (one peanut).

Increased payoff but no social information (IP) group. Testing was terminated after participants had completed 115 solutions. This termination point was more than 100 beyond the average number taken before switching in the IPSI group (median = 13.5), and exceeded the maximum number taken by any IPSI individual before switching to the pull handle (range of 1-114; Table 2).

Coding and analyses

Training and testing phases were narrated and visually recorded using a HC-920 Panasonic camcorder, with responses coded through video analysis. A slide or pull behavior was coded when a participant manipulated only the slide or pull handle respectively. Manipulation of both handles was coded as 'both'. Convergence on the pull handle occurred when an individual used the pull technique on three consecutive occasions. Reversions were using the slide handle or both handles once a participant had switched to the pull technique.

Data were analyzed using Bayesian methods generated by the 'rethinking' package in R (McElreath, 2016), which was used for analyses throughout the studies reported. Supplementary Material describes the analyses in detail, and reports the results of alternative methods of statistical analyses, including a frequentist approach. Throughout analyses, a 95% confidence (or credible) interval is reported. This is the interval between which 95% of plausible values lie. The average value reported is the most probable of all these. Predictions generated by modelling procedures are also reported. These predictions are based on the sample data and attempt to capture population level behaviors. Deviation of the outcome of these predictions from the sample data are reported in the Supplementary Material. Model comparison techniques are also used to construct and choose between different models of the data. This involves inputting different combinations of parameters and seeing how well each predict the data in comparison to one another. We report here on the models which carry most of the Akaike weight (i.e. best predict the data). The model was fitted as the proportion of pull solutions out of the total number of responses (pull, slide and both), as predicted by the absence or presence of social information and increased payoff.

Results

Participant inclusion

Eight individuals in the IPSI groups met criterion for inclusion, six in the SI groups and five in the IP group.

Solutions used

In the IPSI groups, all chimpanzees switched to using pull on the median 14th solution attempt (range 1-114). During the transition of switching, individuals used both handles per solution a median of two times (range 0-9). There was little to no reversion to the original slide method, with only two individuals ever using the slide handle after switching (*Cr* used the slide method once in his subsequent 81 solutions, and *Cea* on three of her 84). Use of both handles per solution was rare post-switch (median = 2.4% of total post switch solutions, range = 0 - 4.8). In the SI groups, where the pull handle resulted in the same reward as the slide, four of the six individuals never manipulated the pull handle. *Chu* used the pull handle once on her first trial. *Ga* used both the pull handle and the slide handle, but with a preference for his original slide technique (sliding in 199/328 solutions). In the IP group, who had not witnessed a model perform the more productive pull solution, no individual discovered it. Testing data are summarized in the Table 2.

Insert Table 2 about here

Regression models

The model that best described the relationship between predictors and outcome was

$$\text{Pull Total} \sim \text{Binomial (Total solutions, p)}$$

$$\text{Logit(p)} = a + a[\text{Individual}] + bip*IP + bsi*SI + bipsi*IP*SI,$$

In the full model above, *a* is the value of the average intercept, *a [individual]* is the intercept deviance for each participant (allowing partially pooled variance), *bip* is the value of the coefficient of the effect of **I**ncreased **P**ayoff, *bsi* is the value of the coefficient of the effect of the presence of **S**ocial **I**nformation, and *bipsi* is the value of the coefficient of the interaction between the presence of a solution with an **I**ncreased **P**ayoff (*IP*) and the presence of **S**ocial **I**nformation (*SI*) regarding the availability of an alternative solution. Coefficients are summarized in Table 3, and indicate no credible effect of either main effect. In support of this conclusion, models which did not include the main effects, that is, just the interaction effect, gained 39% of the Akaike weight, indicating that solution choice of Pull is largely affected by the interaction effect. However, as the full model gained most of the Akaike weight (61%), we summarize the expected proportion of pull solutions for each condition in Figure 2, with only IPSI groups predicted to use the pull solution. In sum, results indicate a clear interaction effect of increased payoff and social information, with no important main effects of either factor alone. Additional details of the analyses and results can be found in the supplementary materials (pages 2-6)

Insert Table 3 about here

Insert Figure 2 about here

Discussion of Study 1.1

IPSI chimpanzees relinquished a highly established, but simple foraging behavior in favor of an alternative, simple solution. Behavioral optimization required both a payoff incentive (Haun, Rekers, & Tomasello, 2014) and social information of the more productive alternative (summarized in Figure 2). However, although there is a strong effect of social information, the lack of discovery in the asocial controls (IP individuals) is not likely due to an inability to perform the pull technique: participants likely just did not realize (and did not explore to discover) that the pull handle was an available solution. This suggests that having a highly practiced working solution may hinder exploration of alternatives (cf Bonawitz et al., 2011; Wood et al., 2013). However, when social information is available, this may be capitalized upon to encourage exploratory behavior, and more productive solutions thus subsequently acquired (Montague, King-Casas, & Cohen, 2006; Toelch, Bruce, Meeus, & Reader, 2011).

Most chimpanzees used both handles during the transition of switching to the pull technique. This may be a result of trial and error learning, or of some failure to completely inhibit use of the slide handle in the first instances of using the pull technique. Although reversion to using the slide handle was rare, participants occasionally employed use of both handles post-switch. The use of both handles during transition and reversions draws parallels with suggestions that children, when learning new problem-solving strategies, have competing representations of these strategies, which overlap and compete not only during periods of transition, but over extended periods of time (Siegler, 1996).

While participants showed a ready ability to change their method of solution, it remained to be determined if having a well-established but simple prior solution hindered behavioral optimization in IPSI individuals through delaying convergence on the pull technique.

Study 1.2. Biways box: Does having an established but *simple* solution hinder adoption of the *simple,* more productive alternative?

In study 1.2, the numbers of solutions performed before converging on the more productive pull technique were compared between the IPSI individuals of study 1.1 and new, solution naïve participants: chimpanzees who had no prior, sub-optimal, solution to the Biways box.

Methods

Testing phase

Increased payoff but solution naïve (SN) groups. The box was presented to two groups, in which nine individuals altogether participated, with both the slide and pull solutions open to discovery, with the slide technique resulting in one peanut, and the pull producing one peanut plus 2-3 grapes. A high-ranking model trained on the pull technique was present in each group. As we were interested in how having a prior solution affected behavioral optimization, testing for SN groups was terminated once participants had converged on the pull technique (pulling on three consecutive occasions), with convergence seen as optimization.

Analysis

The number of attempts taken to converge on the optimum solution was compared between IPSI participants in Study 1.1 and SN individuals using a log-linear regression model to model the effect of experience.

Results and discussion of Study 1.2

Experienced individuals (IPSI) took a median of 13.5 (range 1-114) solutions to optimize their behaviour by using the pull solution; naïve individuals took a median of only 1 (range 1-43). Analysis revealed that the lower limit of the 95% confidence interval of the effect of experience with a prior, alternative solution was close to zero (coefficient mean of 5.5, 95% confidence interval of 1.9 to 16.1). Although Naïve individuals were predicted to converge on the pull behavior a median of 10 solutions earlier (95% confidence interval 1-29), model comparison suggests having a prior solution may not have had a credible effect, as models with and without prior solution as a variable were given similar weight, (Akaike weight of 0.58 and 0.42 respectively) i.e. describe the data almost equally as well (Table S7). This indicates a potentially weak effect of having a prior solution. Alternative analyses (frequentist and Bayesian estimation) were run and do not support an effect of prior experience. This indicates that having a well-established, but simple solution may nevertheless not have a strong impact on behavioral conservatism, or perseveration, with a well-known, but sub-optimal foraging behavior. See Supplementary Material pages 6-9 for further analyses and results.

To further examine the causes of behavioral conservatism, the complexity of the initial solution was increased in study 2.

Study 2.1. Pitfall box: Does having an established but *complex* solution (Solution A) hinder adoption of a more complex solution (Solution B), when inhibition of A is *not* required

As perseveration within the human literature is linked to cognitive load and solution complexity, chimpanzees were trained to extract a small reward from the Pitfall box described below, using a complex solution. A mid-high ranking, female conspecific introduced a simple addition to the solution, which improved productivity. Behavior was subsequently investigated over ten hours of testing. Unlike the Biways box, this solution involved a multi-stepped procedure, and was not one that could be readily discovered. In particular, chimpanzees showed difficulties in the learning of one novel action involving the removal of a defense block. Due to the incorporation of this novel element, and the multiple, non-arbitrary steps required, we propose that the initial solution for the Pitfall box was more complex than that needed for the Biways box.

Methods

Participants

Participants were group housed at the National Center for Chimpanzee Care (N=24, 10 males, mean =31.9 years, range: 19.8 – 50.9; demographics in Table S8).

Apparatus

A transparent foodbox (Figure 3) was structured on two levels, with a small reward on the top level (half a peanut) and a larger reward on the bottom (two peanuts). This was placed in the center of a large, transparent apparatus (Pitfall box; Figure 3– only the right side of the apparatus was used in these studies). This foodbox could be progressed along the Pitfall box using fingers via an open access slot on the front (from the chimpanzee's perspective). Three doors were located on the front of the apparatus (only Doors 1 and 2 were relevant to these studies), which could be opened to gain access to the reward within the foodbox. To progress the foodbox to Door 1, a block defense had to be pushed out of the foodbox's path. A pit (or trap) was located between this block and Door 1, which could be opened or closed by the experimenter.

Insert Figure 3 about here

Training phase

Increased payoff with social information (IPSI) groups. 23 individuals across four groups were given the opportunity to participate. Of these individuals, 10 met criterion for inclusion (range of 2-3 individuals per group). Chimpanzees were trained to solve the task using a 'No Door Solution' by ferrying the foodbox to Door 1, removing the block defense along the way. At Door 1, the participant could reach in via a small access point cut into the door and take the small reward from the top shelf of the foodbox. The large reward was in view, but was inaccessible as all doors were locked shut. Further, the roof of the pit was closed over, and so all food reward passed safely over the pit without falling into it (Figure 4). Participants had to perform this solution 20 times to meet inclusion criterion.

Insert Figure 4 about here

Initially, the designated model within each group displayed this complex method over one hour of training; however, it became apparent that chimpanzees were finding it difficult to learn this solution, and in particular, the removal of the block defense. Removal required a hard 'poke' to the block, which caused it to shoot out the back of the apparatus. Many failed to perform this action, instead repeatedly pushing the foodbox against the block to no effect. To help solution acquisition, participants were given the opportunity to separate voluntarily for further human demonstrations and scaffolding of the solution (this was required for all but one participant). No verbal praise or reward was given for any part of the solution, other than the final retrieval of reward from the foodbox at Door 1. This ensured that particular elements of the solution were not themselves associated with some reward.

Once an individual had extracted the small reward, the apparatus was left against the mesh for a further 5 seconds. This extended time meant that there was opportunity to explore the apparatus in training, thus reducing spurious exploration in subsequent testing sessions

Increased payoff with no social information (IP) group (N=6). To examine the effect of social information on behavioral change, six individuals were offered the opportunity to separate voluntarily for training on the No Door Solution, following the procedures above. If an individual did not wish to separate, that individual was trained in the presence of other group members, providing there was no interference by those individuals.

Testing phase

Increased payoff with social information (IPSI) group (N=10). Door 1 was unlocked. The model performed a new, more productive solution (Door 1 Solution) in her group over ten hours of testing and open diffusion. All participants observed the model before performing any solution (Table S11) and were free to participate throughout the testing period. This solution involved using the No Door Solution with the addition of pushing Door 1 upwards, giving access to the previously inaccessible large reward (Supplementary Video 3; Figure 5). Once the participant extracted any part of the reward, the apparatus was left against the mesh for 5 seconds, allowing further exploration and ensuring that failure to use Door 1 was not due to a lack of opportunity.

Insert Figure 5 about here

Increased payoff but no social information (IP) groups (N=5). Individuals were offered the opportunity to separate for testing. Door 1 was unlocked, and individuals were given up to one hour (over 20 minute sessions) to discover Door 1.

Analysis

To investigte the effect of social information on behavioral optimization, the number of attempts taken to converge on the optimum solution was compared between IPSI individuals and IP individuals, using a log-linear regression model. Further details on this model and addtitional analyses using Bayesian estimation and frequentist methods are reported in the Supplementary Material.

Results

Participant inclusion

Ten individuals in the IPSI groups met criterion for inclusion, and six in the IP groups. All chimpanzees in the IPSI groups quickly built on their behavior to improve productivity, doing so on their 3rd trial (median; range 1-24). Reversions to the trained solution (No Door Solution) were rare (median 0, range 0-2). Five participants in the IP groups (asocial controls) discovered Door 1 (median trials to discovery = 18.5, range 5-84).

Regression model: effect of social information

It was found that social information facilitated acquisition of the more productive solution by reducing the number of trials taken to converge on the Door 1 Solution (expected median of 12 trials earlier, 95% confidence interval of 3-33 trials earlier), with a model including social information as a variable affecting optimization carrying almost all of the Akaike weight (96%), thus describing the data better than a model without an effect of social information (see Supplementary Material pages 10-13 for further analyses and results)

General flexibility

Chimpanzees employed variants of the same solution throughout testing, changing the order of the actions required for solution (Table 4). Participants also pre-emptively removed defenses (the block and Door 1 - median of 8 number of pre-emptive moves, range 6-51).

Discussion of Study 2.1

Here, we tested if chimpanzees would show behavioral conservatism when adding a simple addition to a complex solution. That the original No Door Solution was complex in nature is supported by the difficulty chimpanzees had in learning it during the training phase. Overall, little evidence of behavioral conservatism was seen on this task. Not only did chimpanzees in the IPSI groups readily build on their complex solution, but employed multiple variants of the same solution (Table 4), and often pre-emptively removed defenses to reward procurement. The accumulation witnessed here was very simple, involving a modification that was well within the behavioral repertoire of these chimpanzees, as demonstrated by asocial controls who also built on their solutions through individual discovery of Door 1. Social information facilitated acquisition of the more productive solution but was not required for acquisition.

One reason for the lack of conservatism seen here may be the simplicity of the modification (i.e. lifting a door); that is, knowing a complex behavior may not result in behavioral conservatism when modification to solutions are simple and do not require learning of new behavioral processes. Another reason may be that chimpanzees *were not required to inhibit* a complex solution, as the Door 1 solution incorporated all elements of the No Door Solution. Human cognitive research has suggested that complex behaviors place a higher load on working memory, which interacts with inhibition processes (Diamond, 2013), potentially through 'using up' shared cognitive resources which may be required for successful inhibition. This results in perseverance with an outdated solution.

Study 2.2. Pitfall box: Does having an established but *complex* solution (Solution A) hinder adoption of a *simple*, more productive alternative (Solution B), when inhibition of A is required?

To examine potential causes of behavioral conservatism further, and the interaction between solution complexity and inhibition, the apparatus was modified so that the pit was opened. This caused the large reward (but not the small one) to fall into the trap if the foodbox was moved over this (Supplementary Video 4), as in the original No Door Solution and now extensively practiced Door 1 Solution. Door 2 was unlocked and could now be opened to retrieve all rewards. Hence, individuals in the IPSI groups could perseverate with their old solution, which would result in a small reward, or they could inhibit their behaviors by not moving the foodbox over the pit, and instead open Door 2 for all rewards (Supplementary

Video 5). Door 2 was nearly identical to Door 1, which all participants had mastered in the previous testing session (Study 2.1: median of 59 lifts, range 23-102).

The effect of social information on convergence on the Door 2 solution, and thus inhibition, was not examined here. The IPSI groups had ten hours of prior experience using the complex solution (No Door and Door 1 Solutions), which was not possible with asocial controls, introducing a confound between the effect of social information and experience with the solution. We compared number of solutions taken by IPSI individuals against solution naïve chimpanzees (i.e. those with no prior knowledge of a sub-optimal solution) to converge on the Door 2 Solution (evaluating the effect of prior solution on optimization). We also considered the number of solutions taken to converge on the Door 1 Solution in Study 2.1 compared to the Door 2 Solution here within IPSI individuals (recording ease of incorporation of a simple modification to a solution when optimization requires building on, versus the inhibition of, a known solution).

Methods

Testing phase

Increased payoff with social information (IPSI) groups. The Door 2 Solution was displayed by the model during ten hours of testing and open diffusion (Figure 6). All participants observed the model before performing any solution. Convergence on the Door 2 Solution was taken as three consecutive Door 2 Solutions, with little or no later use of alternative solutions.

Insert Figure 6 about here

Solution naïve (SN) group (Two groups, N= 8). While social information is unlikely to be necessary for solution acquisition, to rule out the confound of the presence/absence of social information and analyse our data based on the presence/absence of prior experience, two mid-high ranking, female conspecifics were trained to display the Door 2 Solution to their groups. Due to time constraints and monopolization of the apparatus by dominant individuals, groups had a 15-minute group-interaction period with the apparatus before interested participants were offered the opportunity to separate voluntarily (either on their own, or in small groups) until they converged on the Door 2 Solution.

Analysis

To examine the effect of having a prior solution on behavior optimization, log-linear regression models compared the number of attempts taken to converge on the Door 2 Solution between IPSI and SN groups, as well as between the number of solutions taken by IPSI individuals to converge on the Door 1 and Door 2 Solutions (i.e. within subjects comparison, with random effects considered).

Results

Solutions used

IPSI participants used their old solution a median of 29.5 times (range 3 - 105) before switching to use the Door 2 Solution, which they then performed a median of 51 times (range 0 - 90). Solution naïve individuals used only the Door 2 Solution, apart from individual *Kg* who used the No Door Solution once, before discovering the Door 2 Solution.

Reversions and redundant behaviors in IPSI individuals

The redundant lifting of Door 1, or removing the block when reward had already been extracted, were uncommon (median of 6 redundant actions, range 0-26). Reversions were also rare (median 4.5, range 0-8).

Regression model: Effect of prior solution

All IPSI chimpanzees, except individual *Ci,* converged on the optimum solution (median 28th solution, range 4 - 99), and naïve individuals on their median 1st solution (range 1-2).

Prior behavior credibly delayed adoption of the optimum behavior (regression coefficient of 11.8, 95% confidence interval of 6.5 - 21.5), with naïve individuals expected to take 14 fewer solution attempts (median, 95% confidence interval 8-24 fewer attempts; model predictions are presented in Figure 7). Model comparison gave all the Akaike weight to a model which included an effect of prior solution i.e. a model without prior solution as a factor does not adequately describe the data.

Further details on these models and addtitional analyses using Bayesian estimation and frequentist methods are reported in the Supplementary Material pages 14-18.

Insert Figure 7 about here

IPSI individuals are expected to take credibly more solutions (median 13, 95% confidence interval of 7 to 26) to converge on the Door 2 Solution than the Door 1 Solution of Study 2.1 (coefficient of effect of door location= 5.8, 95% confidence interval of 4.3 – 7.8; Model including Door location (Door 1 or 2) gained 100% of the Akaike weight; Figure 8).

Insert Figure 8 about here

Biways and Pitfall: summary

We do not directly compare the number of solutions taken by those with a prior, sub-optimal solution to converge on the optimum solution between the Biways and Pitfall participants. Although the manipulation of task complexity is our variable of interest, the effect of a prior solution can only be deduced from analysis that includes naïve individuals faced with the same task, rather than comparisons between tasks. In the Biways task, there is greater overlap in the predicted solutions taken until convergence between naïve and experienced individuals. There is no predicted overlap between these groups in the Pitfall task. In the Biways box, naïve chimpanzees (Biways-SN) did not converge on the optimum solution right away. This indicates that the behaviors seen in Biways-experienced individuals (Biways - IPSI) were perhaps similar to naive controls, and may not have been the result of perseveration. We cannot apply this reasoning to the Pitfall behaviors, as the naïve individuals (Pitfall –SN) immediately converged on the optimum solution and so acted very differently from the experienced individuals (Pitfall – IPSI), who perseverated. We conclude there is a stronger and more credible effect of a *complex* prior solution.

General discussion

Chimpanzees showed relatively little conservatism when behavior optimization involved the inhibition of a well-established but simple solution (Study 1.2), or addition of a simple modification to a well-established but complex solution (Study 2.1). Such changes were facilitated by viewing a model perform the improved solution (Studies 1.1 and 2.1). In contrast, when behavioral optimization involved the inhibition of a well-established but complex solution, chimpanzees showed evidence of conservatism (Study 2.2). This was indicated by two separate findings:

I. Chimpanzees with a prior, sub-optimal solution (Pitfall -IPSI) took longer to converge on the optimum solution than chimpanzees who had no prior solution (Pitfall-SN); and

II. Chimpanzees with a prior, sub-optimal solution (Pitfall-IPSI) quickly optimized their established behaviors when optimization required the addition of a simple behavior, lifting a door (Door 1), to their original solution. However, when optimization again required the lifting of a door (Door 2), but the inhibition of the established solution, chimpanzees took longer to optimize their behavior.

Given that Door 1 and Door 2 were nearly identical, these findings cannot be explained by IPSI chimpanzees not recognizing the affordances of the apparatus, as they quickly converged on opening Door 1 under the same conditions (with a pay-off incentive and social information). Nor can results be explained by chimpanzees not knowing *how* to open Door 2, as the opening process was the same as for Door 1, and readily discovered by solution-naïve chimpanzees. We therefore conclude that behavioral conservatism was caused in this case by a failure to inhibit a well-established solution. Further, given that chimpanzees showed a stronger ability to inhibit their established solution when that solution was simple in nature (Study 1.2), we further propose that behavioral conservatism may be context dependent: behavioral conservatism is not due to an inhibition problem per se, but rather the inhibition of complex behaviors. Complex behaviors very likely place a higher demand on cognitive processes, such as working memory, which may limit the resources needed for inhibition (Halford et al., 1998). Thus, in line with human research, conservatism may be caused by limited cognitive resources. As reviewed in the introduction, we suggest that variation in task complexity contributes to the divergent findings within the primate literature on chimpanzees' behavioral flexibility, and the results reported above provide direct evidence to support this contention.

Habit formation and chunking

A further alternative hypothesis would be that the original behaviors in both Biways and Pitfall were so well practiced that they became habitual. In habit formation, complex action sequences may be 'chunked' into a single executable unit. This may reduce cognitive resource use, as the relationships between actions and outcomes do not have to be held in mind, and are thus potentially more resilient to outcome-dependent change (see Smith & Graybiel, 2014; 2016 for a review). Building on a chunked solution may not be as difficult as interrupting or changing the intrinsic contents of the chunk. In the Pitfall study 2.2, participants would have had to do just this: stop part-way along a chunked sequence and insert a new behavior, something they were not required to do in Biways or Pitfall study 2.1. This suggests that complexity of behavior affects behavioral optimization not because of limited cognitive resources per se, but rather because mechanisms such as chunking may reduce cognitive resource use by making complex behavior less computationally demanding.

Although we are not ruling out this alternative, we suggest that the flexible use of multiple solution variants (Supplementary Material Table S10), as well as predominant use of only outcome relevant actions, indicates that the participants may not have been behaving in a merely habitual manner, but were goal-oriented in their behavior. In contrast, the hallmarks of habitual behavior are invariance, or the use of more "stereotypic and routed movements through a task environment" (Smith & Greybiel, 2014, pg 4).

Behavioral complexity and cumulative culture

Cultural behaviors, especially with regard to technologies like those of wild chimpanzees, can be simple, like placing leaves on wet ground as a seat, or show such complexities as the use of tool sets like power tools to open holes and more delicate probes to fish within them (Boesch, Head, & Robbins, 2009; Sanz, Schöning, & Morgan, 2010; Whiten, 2015). Candidate cumulative change in these behaviors typically involves an increase in such complexity, adding elements to existing routines, as in the unusual fashioning of brush tips on stems used to fish for subterranean termites once tunnels have been made using stout sticks, by Goualougo chimpanzees (Sanz, Call and Morgan, 2009). Outside of our own hominin line, such cumulative complexity appears rare (Tennie et al. 2009). Our findings suggest that this may be caused in part by difficulties in relinquishing elements, or interrupting the sequence, of complex routines. Complementary work (Davis et al., 2016) has found that chimpanzees exhibit yet higher levels of behavioral conservatism when behavioral optimization involves not only the partial inhibition of a complex solution (mirroring Study 2.2), but also the addition of a complex element, as opposed to a simple one. In Davis et al. (2016) chimpanzees initially used a hard-learned, multi-stepped, inefficient method of extracting rewards from a puzzle box. This required participants to lift lids and use the underlying finger holes to maneuver a valued token to an extraction point. To solve the task more efficiently, participants could partially inhibit this inefficient method, and add a complex element of pulling open a door, using a hard-to-master pincer movement, at a different extraction point. Most chimpanzees were able to build on their initial, complex solution only by first mastering the additive door pull as an independent solution, and then combining this with the elements of their original, complex solution.

Conclusion

Notwithstanding other vital socio-cognitive adaptations, it is important to consider that whilst chimpanzees may possess some cognitive functions homologous with our own (Beran et al., 2016), it is very likely that humans have a greater ability to hold on to and manipulate more information in working memory (Coolidge & Wynn, 2005; Haidle, 2010; Washburn 2016), whether through quantitative or qualitative changes in cognitive control. Thus, not only can humans learn more complex sequences of behavior but have more resources available to facilitate behavioral flexibility (see also Gruber, 2016). However, in keeping with findings within human developmental literature (e.g. Davidson et al., 2006), chimpanzees appear to also exhibit perseveration as a result of limited cognitive resources in key executive functions.

Taken together, and in conjunction with previous research reviewed above, our results suggest that chimpanzees' conservatism is in part caused by complexities in the behaviors concerned, both when relinquishing complex behaviors, or adding complex behaviors to established solutions, and this may be constrained by cognitive resource availability. We suggest that these behaviors are particularly relevant for cumulative culture, and may partially explain the relative stasis of chimpanzee culture compared to human culture.

Compliance with Ethical Standards

Ethical approval was granted for this study by the UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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Table 1

Group characteristics

Group	Group ID	Participants	Increased payoff	Social info
Increased **P**ayoff with **S**ocial **I**nfo	IPSI	8	Yes	Yes
Same **P**ayoff with **S**ocial **I**nfo	SI	6	No	Yes
Increased **P**ayoff but no Social Info	IP	5	Yes	No

Note: Participants: Number of individuals in each group meeting criterion for inclusion; Increased payoff = Did the pull method result in a higher payoff than the slide handle? Social info = Was there social information available about the pull method?

Table 2

Behaviors in testing phase

Individual	Group	Increased payoff	Social information	Pull solutions	Total solutions
My	IPSI	Yes	Yes	281	296
Cea	IPSI	Yes	Yes	81	97
Ze	IPSI	Yes	Yes	68	68
Sa	IPSI	Yes	Yes	134	193
Je	IPSI	Yes	Yes	21	29
Ti	IPSI	Yes	Yes	25	59
Hh	IPSI	Yes	Yes	58	60
Cr	IPSI	Yes	Yes	83	207
Na	SI	No	Yes	0	298
Ci	SI	No	Yes	0	87
Ae	SI	No	Yes	0	209
Hg	SI	No	Yes	0	158
Chu	SI	No	Yes	1	155
Gs	SI	No	Yes	55	328
Bn	IP	Yes	No	0	115
Tk	IP	Yes	No	0	115
Sy	IP	Yes	No	0	115
Bte	IP	Yes	No	0	115
Pr	IP	Yes	No	0	115

Note: From left to right: Individual: Initials of participant; Group: IPSI = increased payoff with social information, SI = same payoff with social information, IP = increased payoff with no social information; Increased payoff: Did the pull solution result in an increased payoff? Social information: Was social information about the alternative pull solution available? Pull solutions: total number of pull solutions. Total solutions: all solutions used, including pull, slide and both

Table 3

Coefficients of the model parameters for effect of payoff and social information

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-10.40	5.63	-21.55	0.38
bip	-3.15	5.59	-14.06	7.83
bsi	3.98	5.62	-6.68	15.18
bipsi	11.3	5.64	0.06	22.39

Note: Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

Table 4

Solution variants during Study 2.1 testing

Individual	No Door Solution	Block Sequence	Block Pre-empt	Door 1 Solution	Block Sequence	Block Pre-empt	Door 1 Sequence	Door 1 Pre-empt	Food order Small	Food order Large
My	0	0	0	102	81	21	85	17	86	15
Cea	0	0	0	35	29	6	34	1	31	4
Al	23	19	4	94	90	4	93	1	20	71
Na	17	2	15	78	47	31	73	5	61	9
Ci	7	6	1	23	20	3	21	2	22	1
Ae	1	0	1	53	48	5	53	0	27	26
Sa	6	6	0	32	29	3	29	3	28	3
Gs	1	1	0	54	42	12	49	5	44	8
Hh	0	0	0	63	43	20	62	1	28	35
Cr	1	0	1	78	74	4	76	2	67	4

Note: Table cells are shaded (pink) for data relating to the No Door Solution. From left to right: Individual: Initials of participants; No Door Solution: Number of times the participant used the No Door Solution; Block – Sequence: number of times the block defense was pushed out only once the foodbox arrived at the block's location when using the No Door Solution; Block – Pre-empt: the number of times the block defense was pre-emptively removed *before* the foodbox arrived at the block's location; Door 1 solution: Number of times the participant used the Door 1 solution; Block – Sequence: number of times the block defense was pushed out only once the foodbox arrived at the block's location when using the Door 1 Solution; Block – Pre-empt: the number of times the block defense was removed pre-emptively; Door 1 – Sequence: the number of times Door 1 was opened only when the foodbox arrived at Door 1's location; Door 1 – Pre-empt: the number of times Door 1 was pre-emptively opened before the foodbox arrived at Door 1's location. Food order – Small: the number of times the small reward was removed from the foodbox before the large reward; Food order – Large: the number of times the large reward was removed from the foodbox before the small reward.

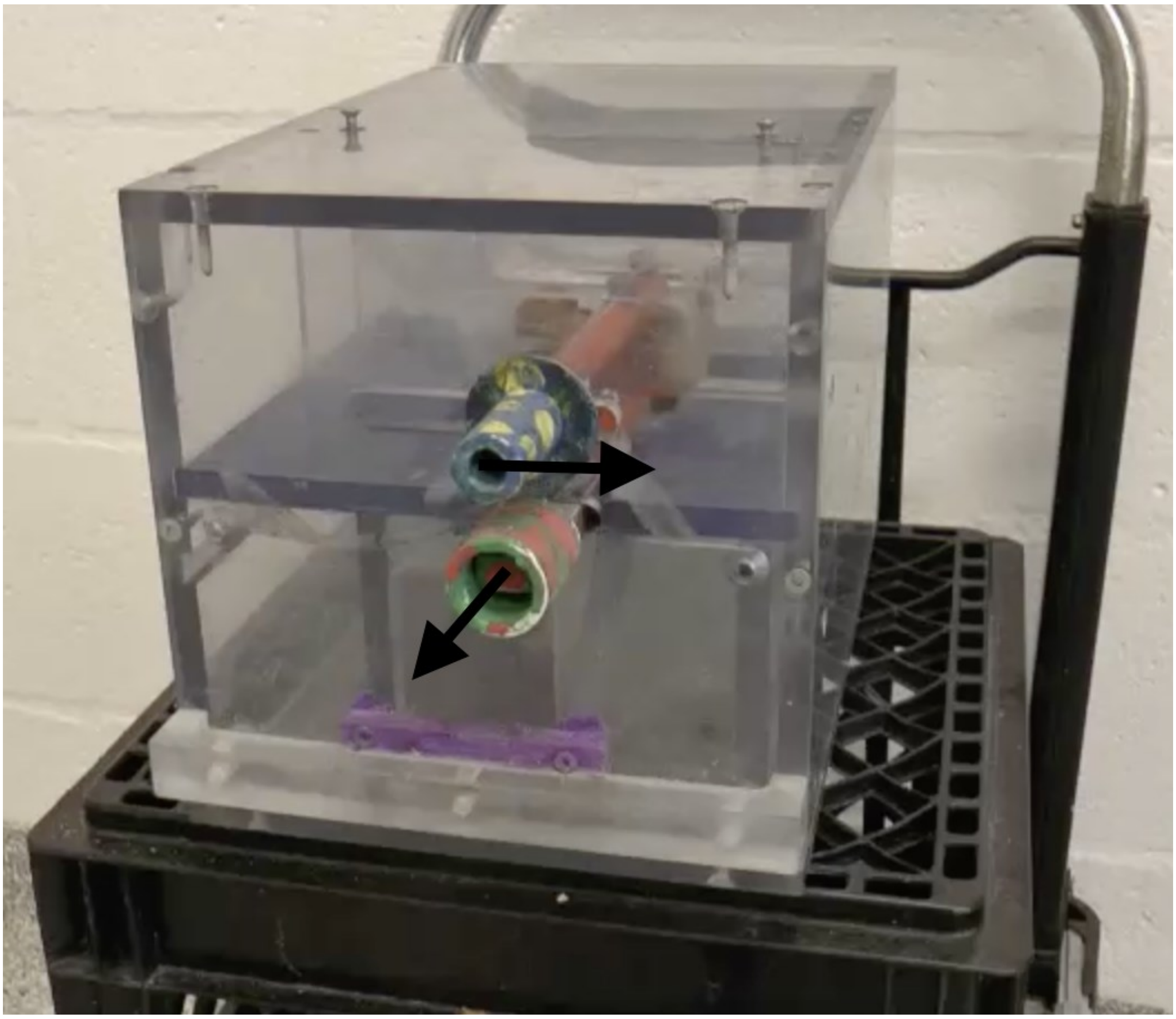

Figure 1. The Biways Box. The top handle can be slid in the direction of the arrow to knock a peanut off the shelf. The bottom handle, when not locked shut, can be pulled outwards to release the peanut plus 3 grapes. The reward is delivered below the handles, where the participant can reach in and remove it.

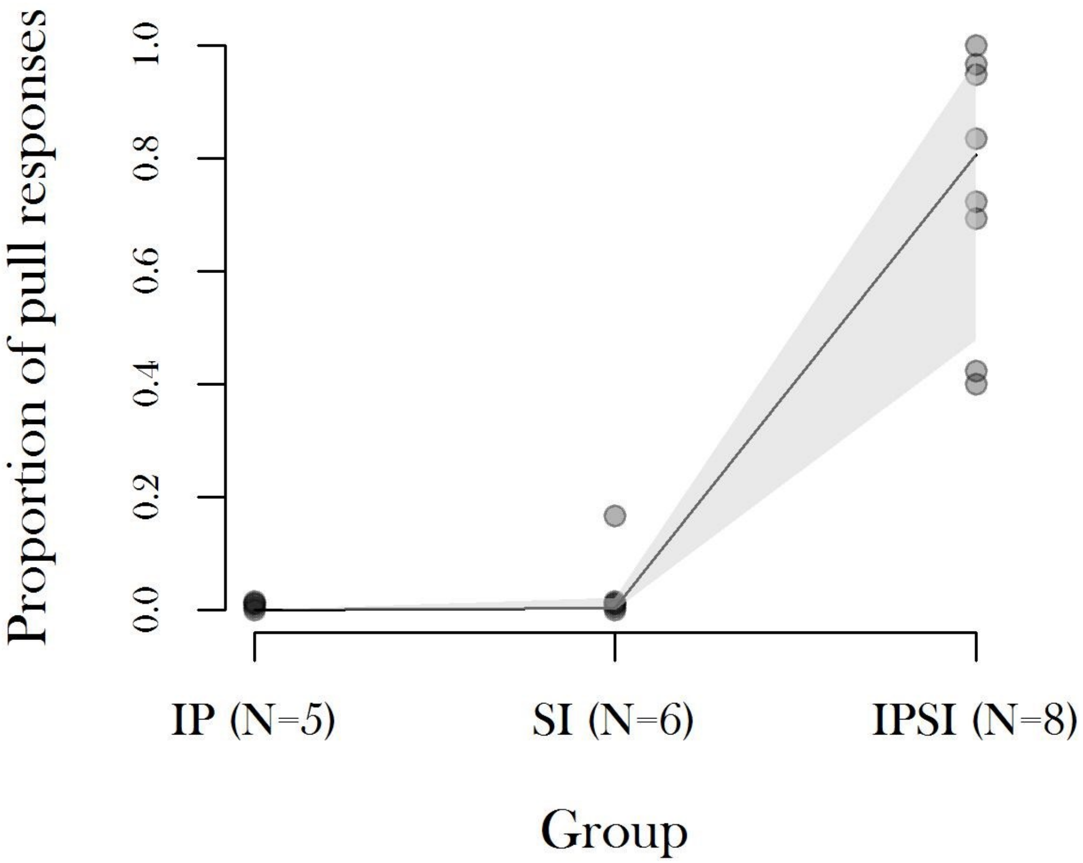

Figure 2. Proportion of pull responses for individuals in the IP, SI and IPSI groups, with N number of participants shown for each group. The line is the mean of the predicted proportion of pull responses, with the shaded area showing 95% confidence intervals. The grey circles (plotted points) are the proportion of pulls for each participant based on the condition they experienced. Plotted points have been 'jittered' around the proportion value of zero for illustrative purposes.

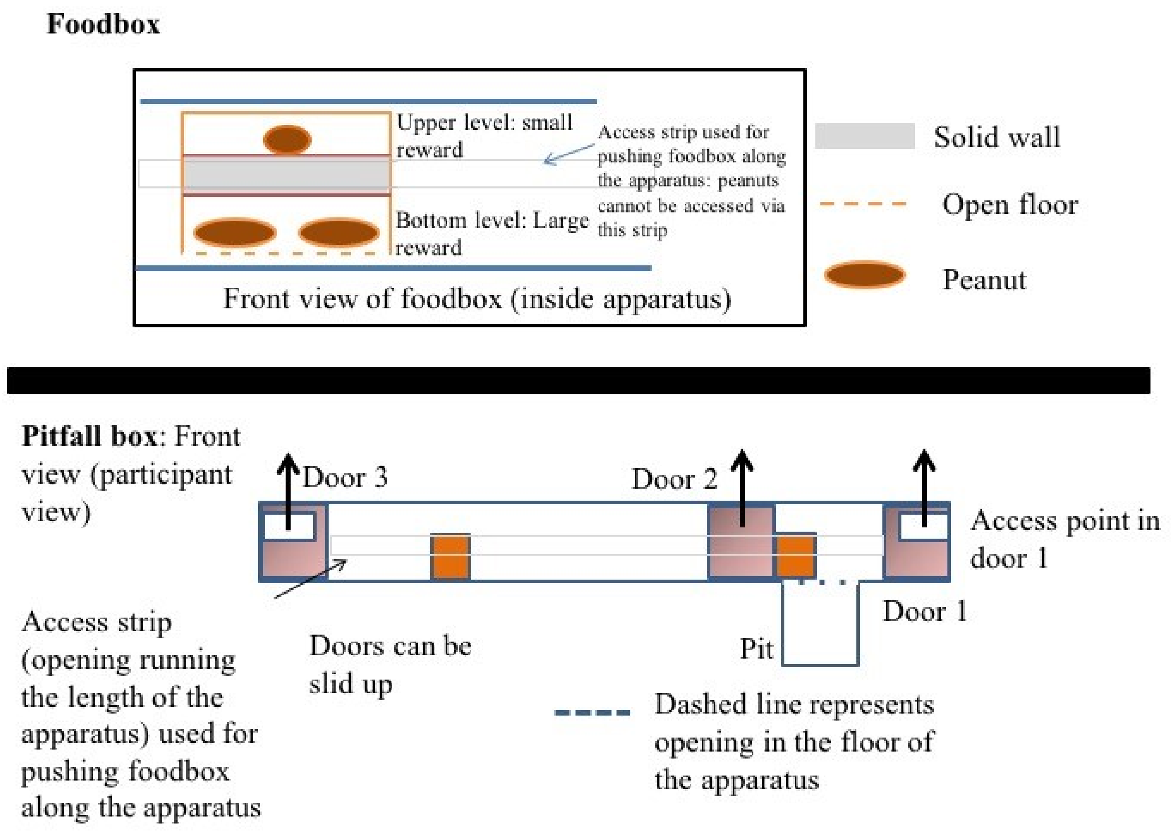

Figure 3. The Foodbox consists of two shelves with reward on each of these shelves. The foodbox sits within the Pitfall box

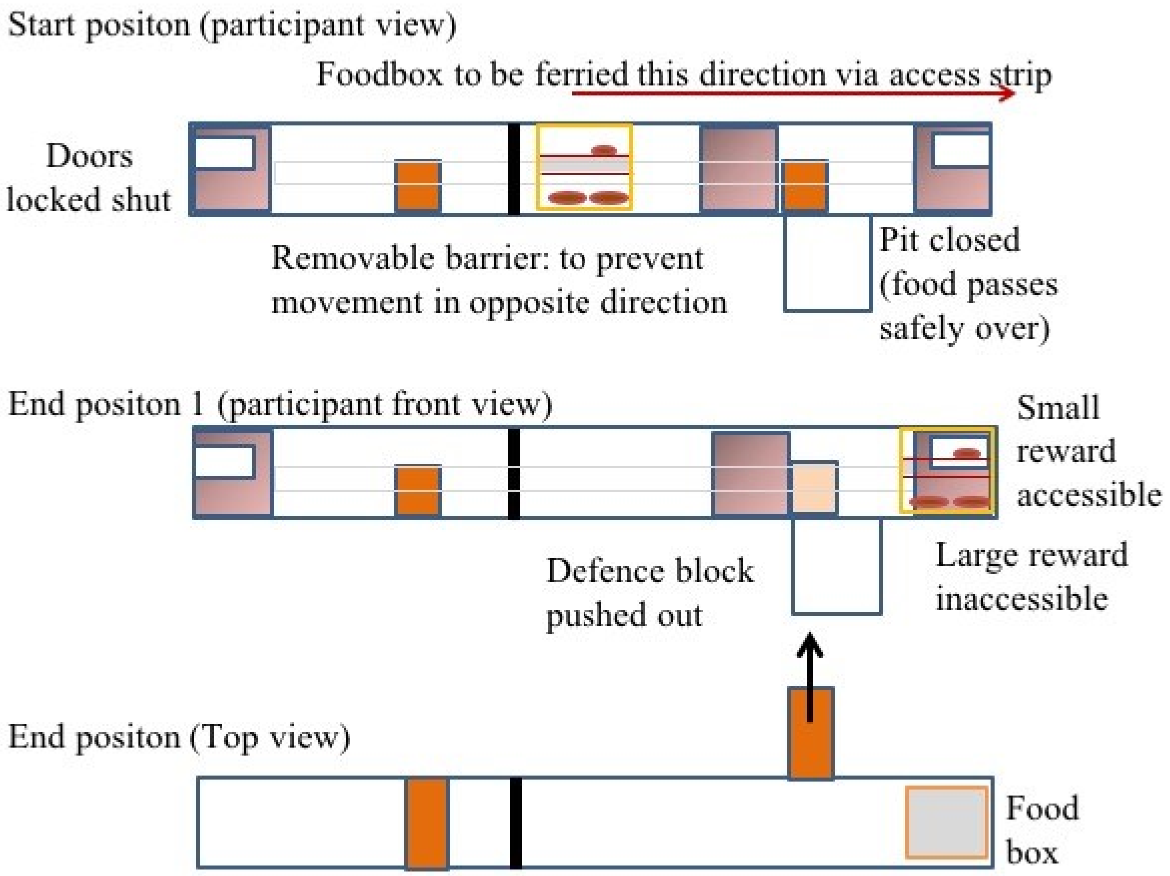

Figure 4. The No Door Solution. With the removal of the defence block, the foodbox can be ferried (via the access strip) to the end of the apparatus. The small food reward can then be extracted at the end via a hole cut into the apparatus (End position 1). No doors can be opened, and the large reward remains inaccessible.

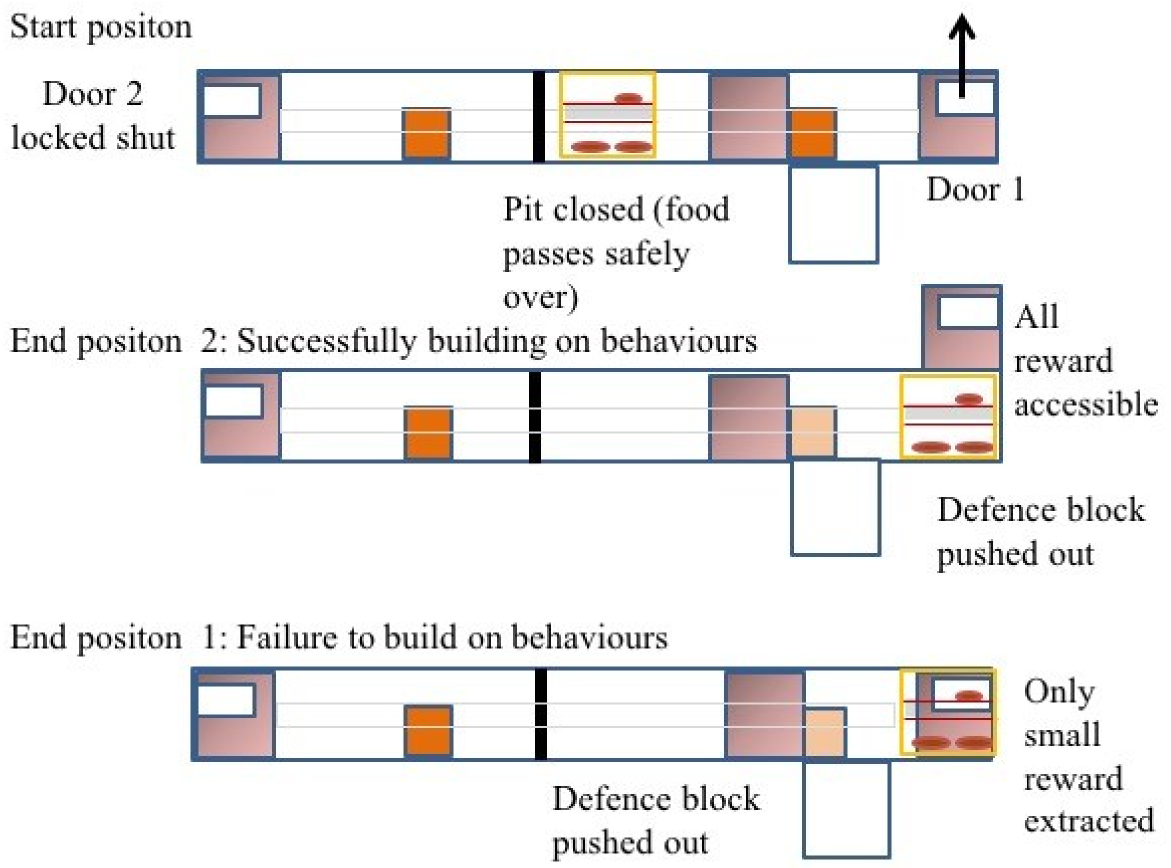

Figure 5. Door 1 Solution. With the removal of the defence block, the foodbox can be ferried (via the access strip) to the end of the apparatus. The small food reward can then be extracted at the end via a hole cut into the apparatus (End position 1), and/or additionally, now Door 1 can be opened, and all the reward extracted (End position 2).

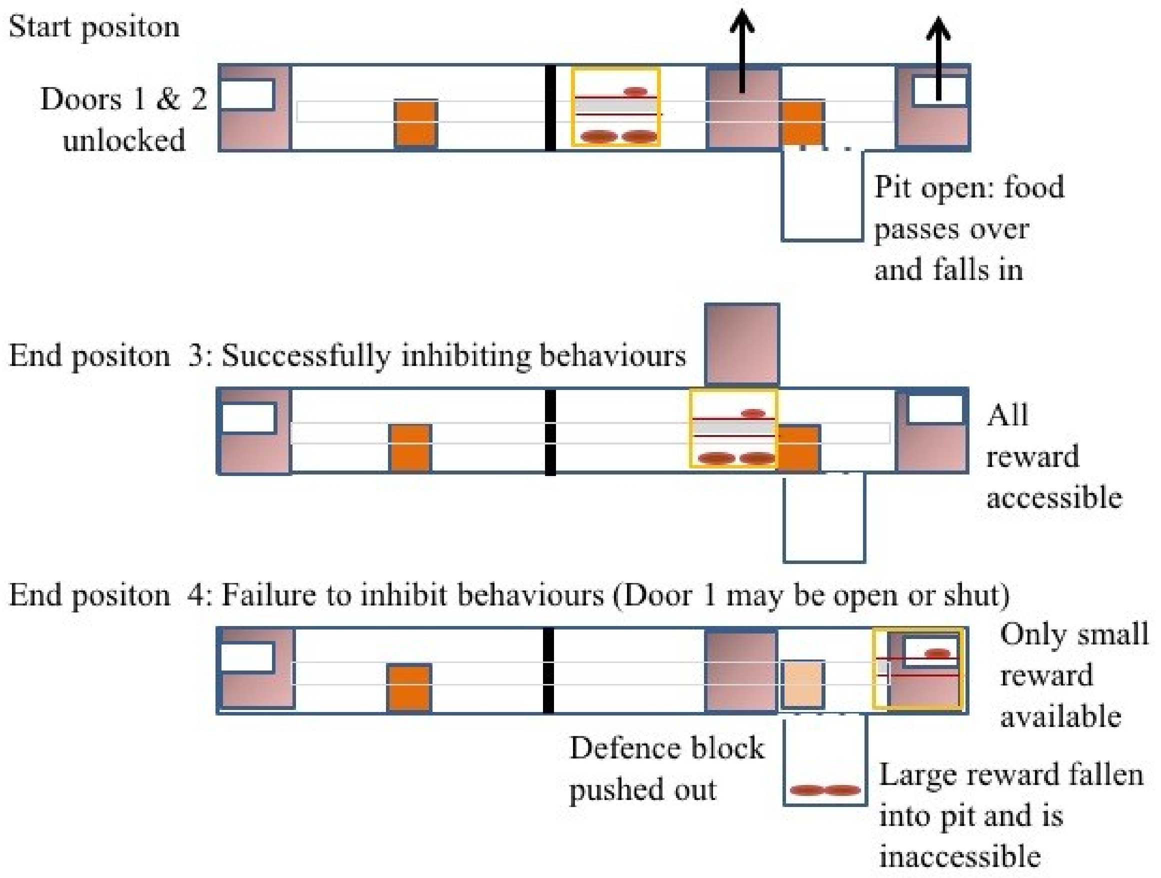

Figure 6. Door 2 Solution. With Door 2 now unlocked, the foodbox need only be moved to the location of Door 2, and the Door opened allowing extraction of all rewards (End position 3). Alternatively, with the removal of the defence block, the foodbox can be ferried (via the access strip) to the end of the apparatus. The small food reward can then be extracted at the end via a hole cut into the apparatus. However, now that the pit is open, the large reward is lost as it is moved to the end of the apparatus (End position 4).

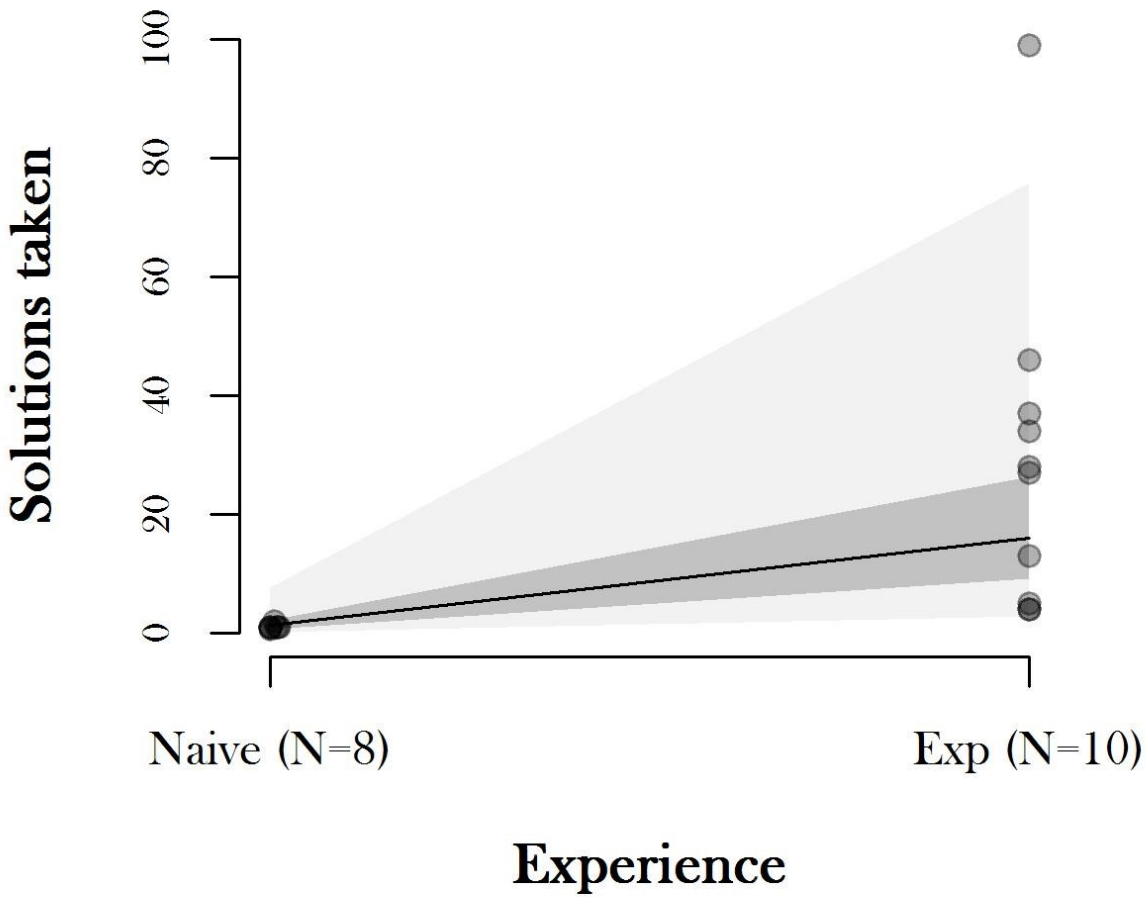

Figure 7. Model predictions for convergence on the optimum Door 2 solution for naïve (SN) and experienced (IPSI) participants. For Naïve individuals, plotted points have been 'jittered' around the value of one for illustrative purposes. The line represents the mean effect of prior solution between the expected number of solutions till convergence on the optimum solution between naïve and experienced individuals, the dark grey area is the 95% confidence limit for this effect. The light grey area is where 95% of the *population* are predicted to fall.

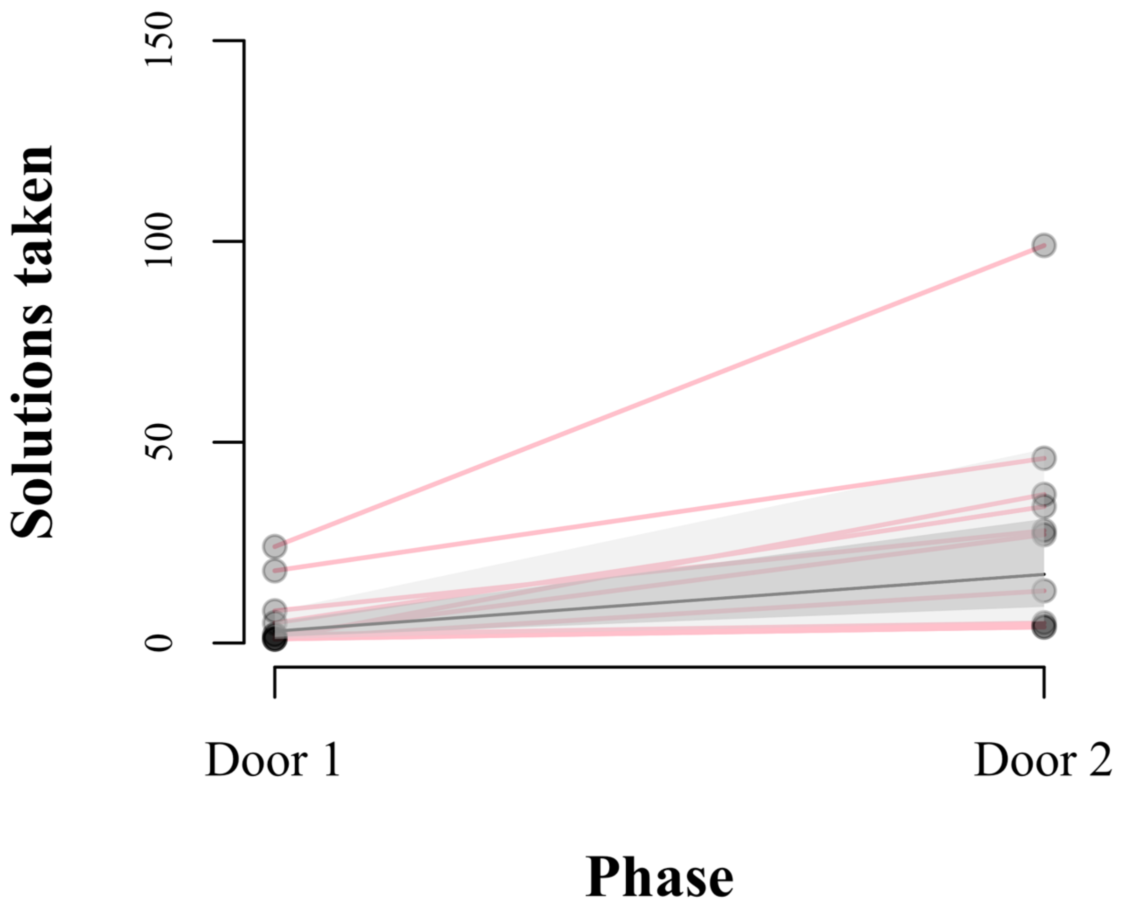

Figure 8. Model predictions for solution taken till convergence on Door 1 and 2 for IPSI individuals. Grey plotted points connected by thin (pink) lines represents the actual observed solution number on which an IPSI individual converged on Door 1 and 2 respectively. The grey line represents the mean effect of door location between the expected number of solutions till convergence on Door 1 (which does not require inhibition) and Door 2 (which requires inhibition) Solutions. The dark grey area is the 95% confidence limit for this effect. The light grey area is where 95% of the *population* are predicted to fall.